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THE APPLICATION OF THE CONCEPTION OF PURE LINES TO SEX-LIMITED INHERI- TANCE AND TO SEXUAL DIMORPHISM¹

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IN the same sense in which our ideas concerning variation and heredity have been entirely revolutionized since 1891, so has a similar change taken place in regard to our theories of sex determination. Sex is now treated by the same methods that are used for Mendelian characters in general. From this point of view I propose to consider to-day three questions, intimately associated. First, the treatment of sex as a Mendelian character; second, the relation between sex and the inheritance of secondary sexual characters; third, the bearing of the recently discovered cases of "sex-limited-inheritance" on the problem of the transmission of characters in general.

Most modern theorists are in agreement that the heredity of sex can be best understood when one sex is regarded as a pure line, or homozygous, and the other sex is treated as a phænotype, *i. e.*, as heterozygous. The experimental evidence has made it plain that in some animals and plants it is the female that is heterozygous, and in other animals and plants it is the male that is heterozygous. Hence have arisen through the necessities of the situation the two following classes of formulæ:

¹From a symposium on "The Study of Pure Lines of Genotypes," before the American Society of Naturalists, December 29, 1910.

	Gametes	
♀♂ Female	♀	♂
♂♂ Male	♂	♂
	♀♂	♂♂
	female	male
♀♀ Female	♀	♀
♀♂ Male	♀	♂
	♀♀	♀♂
	female	male

In certain groups of animals, as in *Abraxas* amongst insects, and in poultry amongst birds, the first scheme is essential to an interpretation of the facts obtained by experiment. In other groups, as in *Drosophila* amongst insects, and in man amongst the vertebrates, the second scheme accounts for the experimental results.

These methods of formulation are open to two serious objections. As the tables show, the combination of ♀♂ stands for the female in one case, and for the male in the other. In order to avoid this apparent contradiction it is assumed that in some groups femaleness dominates maleness, and in other groups maleness dominates femaleness, which seems to me paradoxical at least.

It will be observed also that in the first of these schemes the male carries none of the sexual characters of the female, and in the second scheme the female carries none of those of the male; both of which assumptions do not seem to me to be completely in accord with fact. Cytologists represent these same two schemes in a different way. They represent in the one case the female character by X; and the male by the absence of X. Thus:

	Gametes	
XO Female	X	O
OO Male	O	O
	XO	OO
	female	male

This representation covers the first class of cases where the female is heterozygous. For the second class, where the female is homozygous, the following scheme is

used, in which the female is represented by two X's and the male by one X:

	Gametes	
XX Female	X	X
XO Male	X	O
	XX	XO
	female	male

The XO—OO scheme applies, as before, to the case of *Abraxas* and to poultry, and the XX—XO scheme to the other class of cases. The latter expresses also exactly what takes place in the chromosomes of those groups where two classes of sperm exist (in relation to the X element), as has been demonstrated by Stevens and by Wilson.

In both of these two latter schemes the production of the female is ascribed to the presence of the chromosome X, but in the first formula one X makes the female and its absence stands for the male, while on the second formulation two X's make the female, while one makes the male. In one case XO is female and in the other XO is male. Again we meet with the same paradox as in the first two formulations.

The chief drawback to these formulæ is, in my opinion, the absence of any character to stand for maleness. Absence of femaleness does not appeal to me as a sufficient explanation of the development of a male; for the male is certainly not a female minus the female characters.

Nevertheless, despite these objections I am inclined to think that these two methods of formulation indicate the direction in which we must look for an explanation of the experimental evidence, and that they may be still utilized provided we can so modify them that their inconsistencies can be made to disappear.

It seems to me that if we are to succeed in bringing sex into line with Mendelian methods we must be prepared to grant that there are representative genes for the male condition and others for the female; and we must so shape our formulæ that the female carries the

genes for the male and the male carries those for the female. In fact, I am inclined to think that the evidence forces us to accept Darwin's original view, that in each sex the elements of the other sex are present; a view that has been largely given up by modern theorists (except by Strasburger). I think that we must accept this interpretation for several reasons. Every zoologist is familiar with cases in which the same individual may at first function as a male and later as a female. More remarkable still is the case of the Nematodes in which in some species the female has come to produce both eggs and sperm as shown by Maupas and more recently by Potts, while in another closely related species it is probably the male, according to Maupas and Zur Strassen, that has come to produce eggs as well as sperm. There is further the class of cases where the female develops the male secondary characters and the male those of the female. This class of cases I shall discuss later, for the value of this evidence will turn on whether these secondary sexual characters are represented by independent genes, or are expressions of the presence of one or the other sexual condition; or due to a combination of these two possibilities.

By means of the following formulæ we can meet the requirements that the situation seems to me to demand. If we admit that in the first class one of the genes has become larger than the other female genes, and if we admit that in the second class one of the female genes has become smaller than its sister genes we can account for the results as the following formulæ show:

	Gametes	
	Fm	fm
Fmfm Female	Fm	fm
fmfm Male	fm	fm
	Ffmm	ffmm
	female	male
FmFm Female	Fm	Fm
Fmfm Male	Fm	fm
	FFmm	Ffmm
	female	male

It should be carefully observed that in this scheme the female genes, F or f pair when they meet (allelomorphs); likewise the male genes pair only with male genes. In fact, both genes are carried by all of the gametes. Sexual dimorphism may appear either because one female gene has become stronger than the others, or, because one has become weaker. On the first view we have the case where the female is heterozygous in its female genes; in the latter case it is the male that is heterozygous in its female genes. If in this latter case we assume that the weakened female gene is contained in the so-called Y-chromosome we can then understand how it is that we have a degraded series of this chromosome leading in some forms to its final extinction, for even its disappearance leaves the formulæ unaffected. On the same grounds we may anticipate that in those species in which the X elements are alike in the male, one X in the female may be found larger than its partner, although visible size differences in the chromosomes are not essential to the scheme, since these chromosomes undoubtedly contain many other factors than those of sex whose presence might obscure size relations even when such exist in the sex genes.

These formulæ appear more complicated than those previously given, but in reality they are not so. It is the presence of m in all of the gametes that gives the appearance of complication. If this is omitted, as in the formula given below, the formulæ are no more complex than those given earlier.

	Gametes	
Ff Female	F	f
ff Male	f	f
	<hr/> Ff	<hr/> ff
FF Female	F	F
Ff Male	F	f
	<hr/> FF	<hr/> Ff

The formulæ might be further simplified, if it seemed desirable to do so, by simply indicating the determining factor in each case as shown below; thus:

	Gametes	
FO Female*	F	O
OO Male	O	O
	FO	OO
OO Female	O	O
Of Male	O	f
	OO	Of

But this last simplification is misleading, if the thesis that I shall here maintain in connection with sex-limited inheritance is correct; because the F's and the f's omitted in the last case are supposed to be carried in definite bodies, the chromosomes, which also carry other factors than sex factors, and it is essential to indicate their presence in some way in order that these other factors may have some means of transportation.

In a recent paper on sex determination in phylloxerans and aphids (1909) I discussed at some length different theories of sex determination, and adopted provisionally the view that the outcome is determined by a quantitative factor. The present hypothesis is little more than a further development of this same view,² but I hope in a form more in accord with the Mendelian treatment of the problem. Sex is still represented as the result of a quantitative factor F (or f), but its relation to the male factor is now expressed, for maleness is not assumed, as before, to be no femaleness or less femaleness. Here, as there, more of a particular factor turns the scale towards femaleness in the first class of cases, and less of the female factor allows the scale to turn in the opposite direction in the second class of cases.³

²In 1903 I suggested that in the case of the bee a quantitative factor determines sex, viz., the chromatin; two nuclei producing a female and one a male. Wilson (1905) has identified the quantitative factor with a special chromosome and this interpretation of the quantitative factor is here followed. On Wilson's view the male condition is represented by the absence of the X-chromosome in some cases, and by the presence of only one X-chromosome in the others, (see ante); but on my view the determination of sex is regulated by this quantitative factor in relation to another factor, the male determining element.

³It should be pointed out that these formulæ are in no way related to a suggestion that I made in 1907 in regard to dominance and recessiveness

These formulæ have certain advantages over those now in vogue, first, because the male gene is not ignored as a factor in sex determination; second, that its presence, both in males and females, explains how under certain conditions the male or the female may assume some of the characters of the opposite sex; third, that the paradox of the female being the heterozygous form in one class and the male in the other class is, in part at least, resolved; fourth, that the ease with which species pass from the hermaphrodite condition to that of sexual dimorphism and the reverse is understandable; fifth, that the production of males by parthenogenetic females can be accounted for by the loss of one of the female genes in the polar body; and lastly, we see how there may be two kinds of eggs, as in *Dinophilus apatris*, both of which can be fertilized; for, in such cases the spermatozoa should be all alike.

I do not wish to urge this view too positively, for I am acutely aware that we are only at the beginning of our understanding of the problem of sex determination, but I believe that the difficulties of the current hypotheses must be clearly understood and met if possible.⁴

THE INHERITANCE OF SECONDARY SEXUAL CHARACTERS

From the point of view reached in the preceding discussion let us now examine the problem of the inheritance of secondary sexual characters.

Males are distinguished from females not only by the presence of sperm in place of eggs, but by the presence in general. That view I have entirely abandoned. In the present hypothesis the relation of the determining elements is stated in the same form as in other Mendelian formulæ, with the possible exception that here one gene is represented as larger or smaller than its allelomorphs, and the scale is turned by the mass relation between these female genes and those of the male.

⁴I have not discussed here the possibility of selective fertilization, because if we can explain the facts without this problematical assumption we simplify the problem greatly. Moreover, the evidence brought forward by Payne, Brown and myself, while admittedly insufficient, stands definitely opposed to the view of selective fertilization.

of different kinds of ducts, glands, copulatory organs, or other accessory sexual apparatus; and also by structures not essential to reproduction. These last we call the secondary sexual characters.

It has long been known that in the embryonic development of the vertebrates some of the accessory organs of the male appear in the female, and conversely some of the accessory organs of the female in the male. This evidence seems to me to point with no uncertain meaning to the conclusion that each sex carries the genes of the other. It is however the secondary sexual characters rather than these accessory organs of which I wish to speak now; for, these often appear to be present in one sex only. Are these characters represented in all eggs and sperm or are they by-products of the sexual condition of the animal? Fortunately there is a good deal of experimental evidence that bears on this question, but it is also true that the evidence teaches that the matter must be handled with care, and if I seem to speak dogmatically it is for lack of time rather than for want of caution.

It has been shown by Meisenheimer that removal of the gonads of the caterpillar of *Ocneria dispar* fails to produce any effect, or very little, on the secondary sexual characters of the moth. It would seem, therefore, that these characters are represented in the germ cells in the same way as are other characters, and are not dependent for their development on the presence of the gonads. Some mechanism must exist by means of which the genes of these organs are distributed so that two kinds of individuals are produced. It has been suggested by Castle that the secondary sexual characters may be carried by the Y-element in the formulæ $XX = \text{female}$, $XY = \text{male}$, but this hypothesis fails to explain the results when the Y-element is absent, as E. B. Wilson has pointed out. It also fails to explain how the male secondary sexual organs can appear in the female after castration.

On the sex formulæ that I have suggested it is possible to account for the results, if the genes for these

characters are carried by all cells alike; possibly they go along with the male-group, but this is not essential. Whether they *develop*, or not, will depend on the presence of other genes in the cells. Thus when the Fmfm group is present they will be suppressed, or when, as on the other formulæ, the FmFm group is present. We can understand on this view why in the insects the male secondary sexual organs do not develop in the female after removal of the ovaries, because in this group it is not material derived from this source, but from materials produced in the cells themselves, that bring about the suppression.

It has been demonstrated by Geoffroy Smith that when the young males of the spider crab, *Inarchus mauritanicus*, are infested by *Sacculina* the secondary sexual characters of the female develop. It appears that the parasite produces some substance that inhibits the activity of the male-producing group in each cell, or counteracts some materials produced there, so that the female characters now find the situation favorable for their development. When the young female crab is infected by *Sacculina* she does not develop the male secondary characters, which is in harmony with the view just stated for the manner of action of the parasite.

In birds and in mammals it has long been recognized that some substance is produced in the ovary that inhibits the development in the female of the male secondary sexual characters, for, after removal of the ovaries the male characters may *to some extent* develop. It seems fairly clear that here the female group in each cell fails to entirely suppress the male characters; the inhibiting effect from this source must be reinforced from something produced in the ovary. Whether after castration of the male the secondary sexual characters of the female develop is not so clear, since some at least of the characters that characterize the castrated male may be juvenile. But on my view the possibility exists for the castrated male to produce the secondary sexual

characters of the female, if their development is in part suppressed by substances made in the testis.

The view here presented also allows us to explain how the secondary sexual characters of the male are transmitted through the female, as they may be so transmitted.

THE INHERITANCE OF SEX-LIMITED CHARACTERS

In recent years a new class of facts has been discovered that promises to throw a flood of light not only on the sex-determination problem, but also on the problem of inheritance in general. I refer to the cases of sex-limited inheritance.

We mean by sex-limited inheritance that in certain combinations a particular character appears in one sex only. An example will make this clear. In one of my cultures of the red-eyed fly, *Drosophila*, a white-eyed male appeared. Bred to red-eyed females, all of the offspring, male and female alike, had red eyes. These inbred produced red-eyed males and females, and white-eyed males. In other words the white-eyed mutant transmitted his character to half of his grandsons, but to none of his granddaughters.

Yet this white-eyed condition is not incompatible with femaleness; for, it can be artificially carried over to the female by making a suitable cross. If, for instance, a white-eyed male is crossed with a heterozygous red female, there will be produced red-eyed males and females and white-eyed males and females.

There are certain combinations of sex-limited characters that give results outwardly similar to sexual dimorphism. If a black langshan cock is crossed to a dominique hen, all of the sons are barred and all of the daughters are black. If a white-eyed *Drosophila* female is crossed with a red male all of the sons will have white eyes, and all of the daughters will have red eyes. I have another strain of these flies with *small wings* and still another strain with *truncated wings*. If a female of the former is crossed with a male of the latter strain all of

the daughters will have *long wings* and all of the sons will have *small wings*, like their mother.

These cases conform to Mendel's principle of segregation. Were there time I could show by an analysis of the problem why these sex-limited characters behave in inheritance in a different way from secondary sexual characters, although the results in both cases may be accounted for on the assumption that there are genes in the cells for both kinds of characters. In a word, this difference exists because one of the factors for the sex-limited characters in question is absent from one of the *female determining chromosomes*, while the genes for the secondary sexual characters of the male are contained in other chromosomes, possibly in those that contain the male determinants.

This interpretation of the relation between the X-chromosomes and sex-limited characters makes it now possible to demonstrate a point of great theoretical importance. I invite your serious attention for a few moments longer to this question. Three other characters have appeared in my cultures that are sex-limited; one of these only I may now speak of. A male with wings half the normal length suddenly appeared. He transmitted his short wings to some of his grandsons, but to none of his granddaughters. I tried to see if the other sex-limited character, white eyes, could be combined in the same individual with short wings. As the next diagram shows a red-eyed short-winged male was bred to a white-eyed female with normal wings. All of the offspring had long wings; the female had red eyes and the males white eyes. These were inbred and produced white and red-eyed males and females with long wings, red-eyed males with short wings, and white-eyed males with short wings. In the last case the transfer had been made. The reciprocal cross also given in the diagram is equally instructive.

LWF	—	LWF	Long-winged, white ♀	
SRF	.	O	Short-winged, red ♂	
LWFSRF — LWF				
LWF	SRF	SWF	LRF	♀ Gametes
	LWF	—	O	♂ Gametes
LWFLWF	Long-winged			♀ white eyes
SRFLWF	Long-winged			♀ red eyes
SWFLWF	Long-winged			♀ white eyes
LRFLWF	Long-winged			♀ red eyes
LWF	Long-winged			♂ white eyes
SRF	Short-winged			♂ red eyes
SWF	Short-winged			♂ white eyes
LRF	Long-winged			♂ red eyes
LRF	LRF	Long-winged, red		♀
SWF	O	Short-winged, white		♂
LRFSWF — LRFO				
LRF	SWF	LWF	SRF	♀ Gametes
	LRF	O		♂ Gametes
LRFLRF	Long-winged			♀ red eyes
SWFLRF	Long-winged			♀ red eyes
LWFLRF	Long-winged			♀ red eyes
SRFLRF	Long-winged			♀ red eyes
LRF	Long-winged			♂ red eyes
SWF	Short-winged			♂ white eyes
LWF	Long-winged			♂ white eyes
SRF	Short-winged			♂ red eyes

In both cases the combination is possible because in the female of the hybrid (F_1) a shifting of the gene for long and that for short wing (both carried by the X-chromosome) takes place. This interchange is possible during the synezeis of the two X-chromosomes. On the other hand the male contains only one X-chromosome which has no mate, hence the gene for long wings in the hybrid (F_1) can not leave that chromosome to pass into the male-producing group. If it could do so short-winged females would also appear, but as I have shown they are not present in the second generation.

Interpreted in terms of chromosomes these results can have, in my opinion, but one meaning. During union of homologous chromosomes (during synezeis, perhaps) homologous genes pair and later separate to move to op-

posite sides (or enter the chromosome sometimes one way and sometimes the other). All the genes contained in the X-chromosomes can thus shift in the female because in this group two X's are present. Sex-limited inheritance is only possible where similar conditions exist (either in the male or in the female) and since in man color blindness follows the same scheme as does white eyes in my flies, we have an experimental proof that in the male of *homo sapiens* there is only one X-chromosome, and this, in fact, Guyer has just shown to be the case from cytological evidence. But by parity of reasoning it is the female in *Gallus bankiva* that should have only one X present, but Guyer is persuaded that here too (at least in the race of fowls he studied) the male has only one X-chromosome. There is then in this case a contradiction between the experimental evidence and that furnished by cytology and it remains to see which is correct.

Bateson has shown that some of these cases of sex-limited inheritance can be explained on the grounds that there is a repulsion between the female-determining factor and that character that is sex-limited. The view that I maintain does not involve the idea of a repulsion between unlike elements, not allelomorphic. Spillman's hypothesis also involves this idea of repulsion between unlike elements. On my view, on the contrary, an attempt is made to show how the results may be due to a connection existing between certain material bodies in the egg; a connection that is consistently carried through successive generations, and subject only to the ordinary interchange of genes between homologous chromosomes (when a pair of chromosomes is present).⁵

For several years it has seemed to me that the chromosome hypothesis, so called, could not be utilized to explain the Mendelian results in the form presented by

⁵ The hypothesis advanced here to explain sex-limited inheritance applies also to *Abraxas* if the latter follows the Fmfm scheme and if in the egg there is no interchange between the F-bearing and the f-bearing chromosomes.

Sutton, because, if it were true, there could be no more Mendelian pairs in a given species than the number of chromosomes present in that species. Even if this objection could be avoided⁶ the more serious objection still remained, namely, that with a small number of chromosomes present many characters should Mendelize together, but very few cases of this sort are known. De Vries was the first, I believe, to point out that this objection could be met if the genes are contained in smaller bodies that can pass between homologous pairs of chromosomes; and Boveri has admitted this idea as compatible with his conception of the individuality of the chromosomes. In the case of the inheritance of two sex-limited characters in the same animal we have an experimental verification of this hypothesis.

⁶Spillman's suggestion that the difficulty exists only when it can be shown that more dominant characters can occur in the same individual than the number of chromosomes seems to me only to push back the difficulty.

PURE LINES IN THE STUDY OF GENETICS IN LOWER ORGANISMS¹

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At the meeting of this society a year ago I asked in a paper read,² whether the pure line idea did not deserve agitating a little before this society, and I tried to agitate it. This was because I saw that for practical purposes of future work it would be necessary to make up my mind as to the importance of this idea, and it seemed that other members of the society might be in the same situation and that we might help one another. My method of agitation was to give the apparent relations of the results of work along this line up to that time, to one of the burning problems in our field—the problem of selection. In the few minutes that each of us have here the purpose of agitation can be served and general results brought sharply into view only by naked and dogmatic statements, such as one would never use under other conditions. Such naked and dogmatic presentation has serious disadvantages—felt most decidedly by the author when his critics hold the mirror up to nature. I have therefore at times regretted giving forth this paper. But if it has in any way acted as an irritant to arouse the discussion foreshadowed in our present program, I shall feel that its good results outweigh its painful ones, and that it was worth while after all. We are apparently to have brought before us a part of that “thorough try out” that I asked for, and from a study of our program I think I can see that it is not all to be a pæan of praise for the pure line work. Such illumination and such interest as comes

¹ From a symposium on “The Study of Pure Lines or Genotypes,” before the American Society of Naturalists, December 29, 1910.

² This JOURNAL, March, 1910.

from having both sides presented I believe that we have before us.

What I wish to attempt is to give some concrete illustrations of the answer to the question discussed by Dr. Webber—What *are* genotypes? I note that some of the titles on our program speak of the genotype *hypothesis*, the pure line *theory*. What I wish to emphasize is that these things, whatever we call them, are concrete realities—realities as solid as the diverse existence of dogs, cats and horses. I find in many biologists not working in genetics an incorrigible bent for seeking under such a term as genotype something deeply hypothetical or metaphysical, and for characterizing it therefore boldly as purely imaginative. This is merely because such workers have not the things themselves before them. The genotype is merely a race or strain differing hereditarily in some manner from other races. Neither the idea nor the fact is a new one, and we should perhaps do better to discuss merely the importance of distinguishing in our work the diverse existing strains—rather than to introduce an unfamiliar term for a familiar thing. But investigation has shown the existence of these strains to play a part of such hitherto unsuspected importance that it has seemed worth while to introduce a more precise term, which shall emphasize their importance for work in genetics. In work with a certain lower organism—*Paramecium*—I have found the existence of these diverse strains or genotypes to be the guiding fact, not only for work in genetics, but for all exact work in comparative physiology. I wish to show how this is true.

We must then distinguish clearly these concrete realities called genotypes from any theories that have been built up in connection with them; from any generalizations based on their study up to this time. The existence and importance of genotypes are not bound up with any particular theory regarding selection or any other single point. In lower organisms, at least, genotypes or pure lines are merely the name for certain actual existences that you have before you; for facts that strike you

in the face. We have, side by side in the laboratory, a lot of diverse sets of our organisms, each set derived originally from one individual, and each differing characteristically but minutely from the others—the differences persisting from generation to generation. The behavior and properties of these things are of course a matter for further study. Can selection change them? Can environmental action permanently modify them? These are matters quite distinct from the existence of the genotypes.

To get a clear grasp of the matter, I believe that those not working with lower organisms will find it worth while to try to realize the condition which the investigator in this field has before him. A comparison may help. In lower organisms the genotype is actually isolated, each in a multitude of examples, which live along without admixture, visibly different from all others, for many generations, before again plunging into the melting pot of cross-breeding. In higher organisms we should have the same thing if every rabbit, every dog, every human being, multiplied by repeated division into two like itself, till there were whole counties inhabited by persons that were replicas of our absent president; cities made up of copies of our secretary, and states composed of duplications of the janitor I saw outside. Every human being, as it now stands, represents a different genotype (save perhaps in the case of identical twins), and these genotypes become inextricably interwoven at every generation. It is therefore easy to see how the genotype idea might appeal to workers among higher organisms as a mere hypothesis.

What then are these visible, tangible, isolated genotypes (or races, or strains) of lower organisms, and how are they distinguished? Taking *Paramecium* as a type:

1. Some of them differ in size—the size of each remaining closely constant, under given conditions, for hundreds of generations; for years. This was the first difference observed, and I tried to demonstrate it by giving measurements of successive generations of the different races. But to the worker in the laboratory these differences are evident without refined measurements; the student is at

once struck with the fact that one culture is formed of individuals that are throughout and constantly larger than those of another culture.

And here, in view of that extraordinary cry "no heredity without a correlation table"³ (a cry that at once annihilates most Mendelian evidence of heredity), it may be well to define a little more precisely what is meant by saying that the diverse sizes are hereditary in the different races. It means that if you keep your different genotypes side by side under precisely the same conditions, you will find whenever you choose to examine and measure them, that each has a characteristic size, differing from that of the others. If therefore you follow the diverse lines from generation to generation you will get a set of chains, each with links differing characteristically throughout from the links of the other chains. It means that it is possible to predict the diverse relative sizes that will be found in the different races, and that when you examine them a hundred generations later, you will find the prediction correct. These striking facts *are what are meant* by the statement that the diverse sizes are hereditary in the different lines—and the way to determine whether the statement is true or not is to examine the lines from generation to generation to see if the statement is verified. To neglect this obvious fact; to mix all your lines together and then, in order to find out if size is inherited, to laboriously work out coefficients of correlation by refined biometrical methods—is like cutting serial sections ten microns thick of an eel, in order to find out whether it has an alimentary canal. Persons have been known to so bedevil material with refined histological methods as to quite miss the alimentary canal of an eel. The way to see it is to open the animal up and take a look at it. The way to see diverse genotypes is to isolate them and look at them and measure them and compare them. If the use of correlation tables should succeed in obscuring these striking facts (as should not be the case with proper handling) this would merely show the worthless-

³ Compare Pearson, *Biometrika*, 1910, Vol. 7, p. 372.

ness of this method of attempting to learn the important biological facts under consideration.

2. Some of the genotypes show slight but constant differences in structure, which I shall not dwell upon here.^f

3. They show most varied differences in their physiological characters. These physiological differences may go with differences in form and structure, or apparently they may not—so that we find types that differ, so far as detectable, *only* in physiological peculiarities.

This fact becomes of great practical importance for all physiological investigations, as a few examples from *Paramecium* will show:

(a) The races or genotypes differ in the conditions, both external and internal, that induce conjugation. A worker, using a certain strain, works out the conditions inducing conjugation and gives precise directions for accomplishing this. His colleague, with another strain, finds this work all wrong, and the controversy on this ancient question continues. One of my strains can be absolutely depended on to conjugate monthly if certain definite conditions are furnished; another under the same conditions never conjugates; others show intermediate conditions. These differences require no biometric methods for their demonstration.

(b) Again, the genotypes differ in rate of multiplication; under the same conditions some divide once in twelve hours; others once in twenty-four or more hours; others have intermediate periods.

(c) The genotypes differ as to the conditions required for their existence and increase. Several strains, outwardly alike, living in the same medium, are cultivated side by side on slides, in the usual hay infusion. One flourishes indefinitely. Another multiplies for ten generations, then dies out completely, and this is repeated invariably, no matter how many times we start anew our

^fFor a detailed, illustrated account of the characters, both structural and physiological, of these races, see Jennings and Hargitt, "Characteristics of the Diverse Races of *Paramecium*," *Journal of Morphology*, December, 1910.

cultures of this genotype. A third lives along in a sickly way, barely maintaining its existence.

Thus we get in our laboratory striking cases of natural selection between genotypes. To recall our comparison with human beings, if we could mix an entire community composed homogeneously of, let us say, Roosevelts, with another of copies of your ash man—which would be likely to survive? If we place together in the same culture two genotypes of *Paramecium*, as I have many times done, almost invariably one flourishes while the other dies out. This ruins many a carefully planned experiment; it must take place on a tremendous scale in nature.

What distinguishes the different genotypes then is, mainly, a *different method of responding to the environment*. And this is a type of what heredity is; an organism's heredity is its method of responding to the environmental conditions. Under a given environment the genotype *A* is large, while the genotype *B* is small. Under a given environment the strain *C* conjugates, while *D* does not. Under a given environment the strain *E* divides rapidly, *F* slowly or not at all. The various strains thus differ hereditarily in these respects, and we may say that the differences are matters of heredity. And yet we can get these same contrasts within any genotype (as our diagram illustrates), by varying the environment. The genotype *A* under one environment is large; under another it is small. Under one environment the type *C* conjugates; under another it does not. Under one environment *E* divides rapidly; under another, slowly. Are then size, conjugation and rate of fission after all determined by heredity or by environment? Such a question, when thus put in general terms, is everywhere an idle and unanswerable one. All environmental effects are matters of heredity when we compare types differing in their reaction to the environment; all hereditary characters are matters of environmental action when we compare individuals of the same heredity under effectively different environmental conditions.

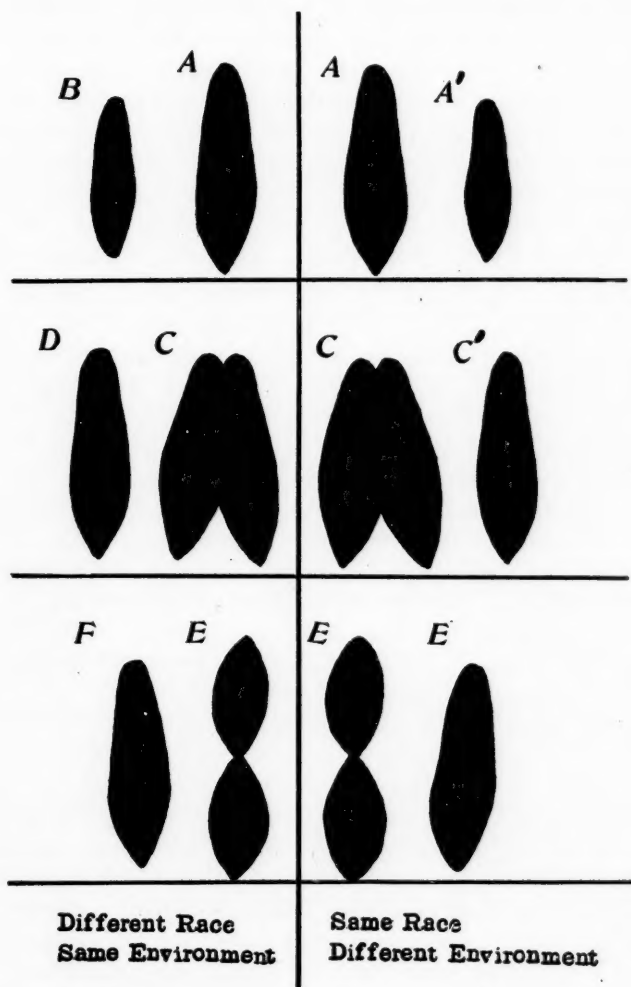


DIAGRAM TO ILLUSTRATE THE RELATION OF HEREDITY TO ENVIRONMENTAL ACTION IN DETERMINING CHARACTERS. (See text.)

Heredity has a meaning only when we (explicitly or implicitly) compare two concrete cases; when we say: To what is due the *difference* between these two cases? Otherwise we can demonstrate either that all character-

istics are hereditary (as we heard maintained at Woods Hole some summers ago); or, with Brooks, that there is no such thing as heredity. If we always compare two concrete cases, asking to what is due the difference between them, and remembering that a difference in heredity means different response to the same environment, we shall avoid these confusions, and shall find the concept of heredity most useful.

Do hereditary differentiations ever arise within our genotypes, so that from one genotype we get two? In other words, do we get from a single type strains that differ in their behavior under the same environment—the differences persisting from generation to generation? This is of course one of the fundamental questions. The genotypes of *Paramecium*, like those of most other organisms that have been carefully studied, are singularly resistant, remaining quite constant in most respects, so far as has been determined. This is an example of what gives the genotype concept its practical and theoretical importance. This is what is meant by saying that selection and environmental action are usually without inherited effect within the genotype. To find differentiations within the genotypes of *Paramecium*, we must examine certain characteristics that are most delicately poised in their responses to all sorts of conditions; such is the rate of multiplication. Studying carefully this most sensitive character, we find that differences do arise within the genotype. Under given conditions, certain rare individuals are found that divide more slowly than usual, others more rapidly, and these differences are perpetuated from generation to generation indefinitely. How are these hereditary differentiations produced?

The origin of these differentiations is in *Paramecium* as elusive as in most other cases where they have been discovered. Apparently they arise in our organism as a result of conjugation within the genotype. Certainly if after an epidemic of conjugation within the genotype we cultivate many isolated exconjugants, we find a certain small number of strains that differ in their rate of fission

from that which is typical. But the experimental analysis of this matter is still in progress, and conclusions can not yet be drawn.

It is only in rate of multiplication that I have thus far found hereditary differences arising within the pure line, and these but rarely. But this encourages one to hope that the same may be found for other characters when these are extensively studied with sufficient minuteness. The negative results thus far reached do not (as many critics have pointed out) exclude the possibility that rare cases of hereditary variation within the pure line will yet be found. What the negative results have demonstrated is that a very large share of the observed variations in organisms are not hereditary, and that selection based on these variations leads to no result—a conclusion of such great importance as to make the pure line work epoch-marking in character.

Finally, what happens when diverse genotypes mix in conjugation? To my disappointment, I have found this much more difficult to determine for the infusorian than I expected. This is owing to the fact that the conditions for conjugation differ in the diverse genotypes, so that it is almost impossible to get them to conjugate at the same time. Further, in the rare cases where two are conjugating at once, the assortative mating discovered by Pearl results in the two sets remaining separate. Thus I have not yet been able to get crosses between two genotypes whose characteristics are known beforehand; and this will be necessary before a study of inheritance, exact in the modern physiological sense, can be made. On the other hand, it is possible to get conjugations in wild populations that include many genotypes, and to compare the results with conjugations where but a single genotype is involved. Certain most interesting results appear. In these conjugations of mixed populations, a great number of diverse combinations are produced; the variability increases greatly, in size and in other respects. Numbers of the strains produced die, or multiply so slowly that they have no chance in competition with

those that are strong and multiply rapidly. Thus many of the combinations produced are canceled; only the strongest combinations survive. We have then on a most extensive scale an operation in natural selection and the survival of the fittest; the production of many combinations, some of which survive, while others fail. As already set forth, there is some indication of the same process in the case of conjugation within the genotype.

At our last meeting I tried to summarize the facts as to the relation of genotypic investigation to selection; it turned out that much which had been deemed a progressive action of selection was not such; and up to that time the action of selection in modifying genotypes had not been demonstrated. Similarly, I had earlier summarized the facts regarding selection in behavior, showing that it there plays a large part. I have hence suffered the peculiar fate of being belabored as an anti-selectionist in genetics, while subjected in the field of behavior to rough treatment as the champion of selection. What I tried to do in both cases was, to determine how far we had actually *seen* the effectiveness of selection—holding this question quite apart from what we believe *must* occur, or believe will be found to occur when we have seen it. It appeared clear, and still appears clear, that a very large share of the apparent progressive action of selection has really consisted in the sorting over of preexisting types, so that it has by no means the theoretical significance that had been given to it. When operating on a single isolated type it appeared that the progressive action of selection had not been seen. These are facts of capital importance to the experimenter; besides their theoretical significance, they open to each of us the opportunity to direct our efforts upon precisely this point, and so perhaps to be the first to see examples of this fundamental process not yet seen. I hoped to accomplish this myself, but after strenuous, long-continued, and hopeful efforts, I have not yet succeeded in seeing selection effective in producing a new genotype. This failure to discover selection resulting in progress came to me as a

painful surprise, for like Pearson I find it impossible to construct for myself a "philosophical scheme of evolution" without the results of selection and I would like to see what I believe must occur. It is therefore with some pleasure that I am able to record for *Paramecium* this extensive operation of selection among the diverse existing lines, and particularly in this extensive production of new combinations at conjugation, with cancellation of many of the combinations. It would seem that the diverse genotypes must have arisen from one, in some way, and when we find out how this happens, then such selection between genotypes will be all the selection that we require for our evolutionary progress. What I hope, therefore, is that some one on our program, more fortunate than myself, will be able to record seeing the actual production of two genotypes from one, or the transformation of one into another, by selection, or in any way whatever.

Yet even if this is done, we shall make the greatest possible mistake if we therefore conclude that the existence of genotypes is unimportant, and throw the matter aside; for work with a mixture of unknown genotypes will always give confused and ambiguous results, whose significance no one can know. If on the other hand we work with single genotypes, or with known combinations of them, we shall understand what our results mean. And this applies to work in other fields of biology as well as to genetics.

SOME EFFECTS OF TEMPERATURE UPON
GROWING MICE, AND THE PERSISTENCE
OF SUCH EFFECTS IN A SUBSE-
QUENT GENERATION¹

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I MUST preface my remarks by an apology for coming before you with some results which have already been published pretty fully within the past year.² My appearance here may seem the more unwarranted in view of the limited amount of evidence which I am about to offer upon those subjects which form the focus of attention at this meeting, namely heredity and evolution. However, aside from the fact that I am acting at the instance of our president, I will say two things in my own defense. First, the results which I offer, meager as they doubtless are, appear to be the only ones of just this sort which are in evidence at present.³ And secondly, I am bold enough to believe that I have developed a promising method of attacking a few of the many knotty problems which are bound up together in the time-honored question: Are

¹ Read before the American Society of Naturalists, December 30, 1910.

² "Some Effects of External Conditions upon the White Mouse," *Journal of Experimental Zoology*, August, 1909. "The Reappearance in the Offspring of Artificially Produced Parental Modifications," *AMERICAN NATURALIST*, January, 1910. "An Experimental Study of Somatic Modifications and their Reappearance in the Offspring," *Archiv für Entwicklungsmechanik der Organismen*, June, 1910.

³ Since writing this statement, I have received Semon's highly interesting paper, entitled 'Der Stand der Frage nach der Vererbung erworbener Eigenschaften' (Fortschritte der naturwissenschaftlichen Forschung, Bd. II, 1910). From this I learn that some of the more important features of my results have been obtained by Przibram, in the course of experiments upon rats, conducted at about the same time as my own. I have not yet seen Przibram's own report of his work. This confirmation will, I trust, dispel any doubts as to the statistical significance of my own figures, whatever interpretation we may choose to give them.

acquired characters inherited? It is my hope to convince you that the method which I have employed conforms to certain *a priori* requirements, on the one hand, and, on the other hand, is workable in practise. That my results are not thus far more imposing is due, I think, to no defect in the method itself, but to the limitations which encompass a solitary investigator, deprived of some of the generally acknowledged desiderata for successful work in animal breeding, such, for example, as assistants, funds and adequate equipment.

As to the logical requirements for such a test—to begin with, what is it that we are going to test? The “inheritance of acquired characters”?—yes and no. First of all, that threadbare expression itself must be relegated to limbo where it belongs. For, not only does it fail to indicate with any precision the subject-matter of our inquiry, but historically the expression has been applied to a wide range of phenomena, real and alleged. Some of these we now know to be fictitious; others, on the contrary, are acknowledged facts; while others yet are more or less debatable. It is with the debatable group, of course, that we are here concerned. But, even among these, we encounter not one problem but many. Suppose, then, that we drop all vague generalized expressions and consider one more or less restricted problem: *Are specific structural effects, resulting from the action of external conditions upon organisms of one generation ever repeated in the next generation under such circumstances that the immediate and parallel modification of the germ-cells may not be invoked as an explanation?* Under “specific structural effects,” I do not wish to include general conditions of health, metabolism, etc.

What are some of the necessary conditions for a fair test of this question? To begin with, we must effect our modifications in the first generation. And since these modifications, if repeated at all, will probably reappear in a much-diminished degree, it would seem far preferable to select characters which lend themselves readily

to accurate measurement. Qualitative differences, such as those of color or of physiological reactions, do not seem well adapted to such experiments, although they have commonly been the ones dealt with in studies of this sort.

In the second place, we must choose such an organism and such a physical agency that the latter may act upon the former without immediately influencing the germ-cells. This would seem to rule out of consideration as really crucial tests of this problem all experiments, however instructive otherwise, in which modification has been brought about through the influence of foods, unusual in amount or in character. For the effect of these upon the parent body is, of course, a chemical one, and the specific substances responsible for the modifications are presumably free to enter the germ-cells. The experiments of Arnold Pictet upon lepidoptera and of Houssay upon fowls are to be recalled in this connection. Similar considerations apply with equal force to any results from experiments in which invertebrate animals or "cold-blooded" vertebrates have been influenced by temperature. The recent work of Kammerer upon lizards⁴ and that of various investigators upon butterflies and moths occur to us at this point; likewise certain features of Tower's work on *Leptinotarsa*. In such cases, by pretty general consent, we have to do with an "immediate effect upon the germ-plasm," and not with *transmission* at all. Later, I shall inquire a little into the validity of this assumption.

In the meantime, I will point out that for certain classes of animals this objection cannot be raised, at least in its original form. I refer to the so-called "warm-blooded" ones. I am not very well versed in that branch of physiology which deals with temperature regulation, but the published evidence which I have examined seems to show that mammals normally undergo but slight fluctuations of body temperature as a result of even very

⁴ *Archiv für Entwicklungsmechanik der Organismen*, September, 1910.

considerable changes in the temperature of the surrounding atmosphere.⁵

Assuming, provisionally, the truth of this proposition, we may discount in advance the objection that the germ-cells of a mammal may be influenced by differences of temperature *as such*. If these differences affect the germ-cells at all, and it is reasonable to believe that they may do so, they must act upon them indirectly.⁶ I shall revert to this point again shortly.

As some of you may perhaps already know, I have succeeded for several years past in producing very decided quantitative differences in certain of the external parts of mice through the action of widely differing temperatures. . . . (This part of the discussion has been omitted in the printed report, since the results in question have already been fully published.)

In experiments such as those which I am describing, it is obviously impossible to subject a single individual to both extremes of temperature during growth, and to compare the differing effects of these upon structure. We therefore, of necessity, resort to a comparison of averages, based upon as many individuals as possible. If each of the contrasted groups is sufficiently large, and if its members have been taken at random, the presumption

⁵Przibram found that the body temperature of his rats was somewhat raised when kept in a room at 30° to 35° C. This last was, however, considerably higher than the mean temperature of my own warm room, and the limits of physiological adaptability seem to have been overstepped in his experiments. (See Semon, *op. cit.*, pp. 45, 46.) On the other hand, Pembrey (*Journal of Physiology*, 1895) found that the body temperature of mice did not rise appreciably above the normal when the animals were kept at a temperature of 29.5° or even 32.5° C. for an hour or more. The effects of a more prolonged stay were not determined. I have myself recently commenced experiments with mice, using a special clinical thermometer made for the purpose. I have already (January 21) shown pretty conclusively that mice may have almost precisely the same rectal temperature at -6° C. as at +30° C.

⁶The same is true even if humidity, rather than temperature *per se*, is the factor chiefly concerned in these modifications. As stated in my first paper (1909), the relative humidity of my heated room was very much lower than that of the unheated room. Thus far I have not differentiated the effects of these two factors.

is that the mean potential (that is to say, congenital) value of every character is about the same for the two lots. I fully realize that the study of genetic problems by the use of mass averages has recently received a decided set-back, largely through the labors of some of those who have contributed to our present program. But until some one is ingenious enough to produce a strain of parthenogenetic or self-fertilizing mice, I fear that my only practical method of procedure in these experiments is to deal with mass statistics based upon "heterozygous" stock.

It must also be pointed out that the technique of the problem which I am discussing is inevitably different from that involved in the endeavor to find, or to produce, "mutations" or single abrupt deviations from the parent stock, which appear at once in full force, if they appear at all, and thereafter breed true. On the contrary, the distribution of the lengths for the tail, ear and foot, within each of the temperature groups in my experiments, appears to follow the normal probability curve, just as in the case of the so-called "fluctuating variations," whose heritability is nowadays so much in question.

In the splendid paper of Professor Johannsen, to which we listened yesterday, occurs the following statement: "as yet no experiment with genotypically homogeneous cultures has given any evidence for the Lamarckian view, the most extreme 'transmission'-conception ever issued." Leaving aside for the time being the question whether results such as mine, even when every possible defect of technique has been eliminated, are to be regarded as "evidence for the Lamarckian view," let us consider for a moment whether the fact that I have not myself found it practicable to use "genotypically homogeneous cultures" does, in reality, invalidate the evidence which I offer. Apparently Professor Johannsen would hold this to be true. So far as I can see myself, the only difference between results from pure and from mixed lines in the

present case would be this. Individuals belonging to a single pure line would probably respond with much greater uniformity to the effects of an environmental change than would those belonging to a composite stock, consisting of a number of lines. It is quite conceivable that among these last some would respond in a much greater measure than others. Or indeed some might not be affected at all. But here the much-scorned "mass statistics" would reveal the mean tendencies of the two lots, and the resulting data, though confessedly capable of further analysis, would be none the less valuable. If it be objected that the differences between the two averages may be due to the presence in one or both of the contrasted lots of a few "mutants," while the remaining individuals may not have been affected at all, I will only point out, as above, that the frequency distributions are directly opposed to such an assumption.

Having produced modifications of the sort mentioned, it remained to be seen whether these effects persisted beyond the generation immediately influenced. . . . (This part of the discussion, including an account of the method employed, the results, and certain of the possibilities of interpretation, I have thought it best to omit here, in view of the fact that I have covered practically the same ground in statements already published. I will merely note that the offspring of warm-room and cold-room mice, although themselves reared under identical temperature conditions, presented differences of the same sort as had been brought about in their parents through the direct effect of temperature, viz., differences in the mean length of tail, foot and ear.)

There remain two principal alternative explanations, which are not wholly distinguishable from one another, and neither of which admits of being stated except in rather vague terms.

One of these is the assumption that the changes undergone by the parent body are in some way registered in the germ cells, so as to be repeated, in a certain measure, in

the body of the offspring. This conception has taken various forms, commencing with Darwin's hypothesis of "pangenesis." The same general view has recently been restated in chemical terms, and in a manner which is perhaps far less shocking to our common sense.

The other alternative is that of a "parallel induction" or "simultaneous modification of the germ-plasm," through the direct action of the modifying agent. This explanation, as we all know, has been freely used by Weismann and others to account for a considerable range of phenomena, notably the persistence of temperature effects in a second generation of butterflies. The phrase has indeed become so familiar through long repetition that few of us stop to consider just what it implies. "Parallel modification of the germ-plasm?" How can the unformed material of the germ cells be modified in the same manner as certain groups of somatic cells—say in a butterfly's wing—even by an all-pervading influence like temperature? This is obviously not what is intended. What we mean, concretely stated, is this: the germinal matter is so affected by the temperature that, after some hundreds or thousands of cell generations, certain of the resulting cells will show peculiarities in their pigment-producing powers of the same nature as those which arose directly in the somatic cells of the parent. And a most curious feature of this coincidence is that these modified cells are situated in precisely the same parts of the body in the one case as in the other.⁷

Thus do these very simple explanations have a way of losing their simplicity when examined critically. In the present instance, the hypothesis stated may, for all we know, be the one that most nearly represents the truth. But it should be stated frankly, in all its complexity, and not palmed off upon us as a readily intelligible hypothesis, which relieves us of the necessity of adopting an "inconceivable" one such as that of pangenesis.

⁷ Weismann's "determinant" hypothesis offers at least a *formal* solution of this difficulty, but I think that most biologists will agree with me that the solution thus offered is almost wholly a formal one.

In the case of a warm-blooded animal, of course, such an explanation as the foregoing could not be offered without still further modification. It might be conceded that temperature, as such, could not affect the germ-cells to any appreciable extent. But it might, on the other hand, be contended that the effects of temperature, even upon the parent body itself, may not be direct, but may be due to the formation of specific chemical substances, which, through the medium of the blood, may be supposed to simultaneously influence the body and the germ-cells. Thus we should, after all, be invoking a "simultaneous modification of the germ-plasm," as in the case of cold-blooded animals.

Such a conception, vague as it is, has certain decided elements of strength. Let me point out, however, as I have already done more than once, that any such chemico-physiological mechanism as is here assumed would be of nearly or quite the same value for evolution as the "inheritance of acquired characters" in the old sense. An interpretation of this sort might "save the face" of certain speculative students of heredity, but the difference between the two views would have little but academic interest.

At the present time, I am continuing these experiments with mice, and am not only using much larger numbers than hitherto, but am resorting to several variations of the original theme, by which I hope to reduce the number of possible interpretations to a minimum. A friend wrote to me recently, wishing me no end of "good results, *not Lamarckian*." This doubtless represents the attitude of a large number of persons toward the whole subject. By many, anything with a taint of "Lamarckism" about it would seem to be, *ipso facto*, beyond the pale of legitimate scientific investigation, belonging rather to the same category as pre-natal influences, telepathy and the "borderland" phenomena of psychical research. But the dawn of better times is already with us.

In conclusion, let me state that my own attitude toward

this group of problems is one of indecision. If I confess to you, as I am bound to do, that positive results from my own experiments will give me far greater satisfaction than negative ones, this is chiefly because negative results commonly prove nothing. The question would be left very nearly as it was before. This, of course, constitutes a serious defect in my own vaunted method of attacking the problem, a defect which it shares, however, with any other which could be devised. But any results are better than no results, and these problems seem worth a far more thorough testing than they have yet received. The present experiments ought, as Professor MacDougal has pointed out,⁸ and the author keenly realizes, to be subjected to various checks and controls, and to be continued through a considerable series of generations. It is my own fervent hope to be able to carry out such a program.

⁸ Presidential address before the American Society of Naturalists, read at Ithaca, December 29, 1910.

THE MENDELIAN RATIO AND BLENDED INHERITANCE¹

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THE indefatigable efforts of neo-Mendelists have succeeded in bringing numerous cases of inheritance, which had previously been considered incompatible with Mendel's law, into their domain by widening the original limitations. We still have many instances such as blended inheritance which can not apparently be harmonized with the law of Mendel. Recent experiments which demonstrate the existence of various degrees of dominance as well as the mutability of the determinants in their behavior, suggested to the writer that various forms of inheritance might be considered as degrees of modification of the law of Mendel. With this view in mind, I have attempted to obtain some general expression for the underlying principle of the law of inheritance by which means Mendel's original law may possibly be theoretically connected with the other cases. In fact, I was compelled to pursue this investigation in connection with my own experiments on the inheritance of the weight of the central nervous system, though this is not yet ready to present at this time.

In carrying out this investigation, I have assumed that the germ plasm is composed of many factors, the true nature of which is unknown, but which in one way or another determine the characters in the offspring. It is these hypothetical factors which are here provisionally called determinants. With this understanding, we may now proceed to the argument.

Suppose a gamete of one parent after the reducing division contains n determinants, the whole group of

¹ Read before the American Society of Naturalists, December 30, 1910.

determinants being designated p , and the gamete of another parent also contains after the reducing division n determinants, the whole group being designated q . Then in the first hybrid zygote (F_1) there will be contained at the time of the union of the gametes $2n$ determinants. As we know, rearrangement takes place during the maturation of the germ cells and we assume this rearrangement to involve a random sampling by which n determinants are taken from the group of $2n$. From the theory of probabilities we find that $n, n-1, n-2, \dots$ determinants of either parent contained in the gametes of F_1 are proportional to the successive terms of the following series:

$$p^n + np^{n-1}q + \frac{n(n-1)}{1 \cdot 2} p^{n-2}q^2 + \frac{n(n-1)(n-2)}{1 \cdot 2 \cdot 3} p^{n-3}q^3 + \dots \quad (1)$$

The same phenomenon happens in the gametes of the other hybrid parent (F_1) and since the gametic constitution of the two hybrid parents is assumed to be identical with respect to the distribution of determinants (1), the frequency of the various combinations of the determinants in the second hybrid offspring (F_2) will be given by the square of (1) or

$$\left(p^n + np^{n-1}q + \frac{n(n-1)}{1 \cdot 2} p^{n-2}q^2 + \frac{n(n-1)(n-2)}{1 \cdot 2 \cdot 3} p^{n-3}q^3 + \dots \right)^2 \quad (2)$$

which may also be written as follows:

$$(p^2 + 2pq + q^2)^n.$$

This series, or the square of the binomial series, is then the most general expression for the gametic composition of any hybrid arising from a combination of p and q determinants and may therefore be considered as the underlying principle of any law of inheritance where the idea of determinants is used.

It is evident that since the somatic characters in question depend entirely on the behavior of the determinants, the relative frequency of various zygotes, as well as the character of the zygotes, depends on whether p or q de-

terminants are related as dominant and recessive, respectively, or whether they blend.

Suppose p is recessive and q is dominant in the Mendelian sense, we at once obtain from (2) the general expression for the alternative inheritance or

$$(RR + 2DR + DD)^n$$

where n refers to the number of allelomorphic pairs of characters, and the expansion gives a strict Mendelian ratio for any number of allelomorphic pairs of characters.

On the other hand, if we consider that p and q determinants blend with an equal intensity the series (2) will give all grades of hybrid characters between the two parental types, the frequency of which is proportional to the successive terms of a symmetrical point binomial curve, and the maximum frequency will be associated with the midparental types (case of equipotency). Castle's ('09) experiments with the length of the ear of rabbits illustrates this case.

Again let us suppose that p and q determinants blend, but with unequal intensity. According as p or q is prepotent, the zygote will resemble more closely one or the other parent. The frequency of each type of zygote again will be represented by the symmetrical point binomial curve. Thus the present series (2) represents both alternative and blended inheritance according to the behavior of the determinants.

The fact just mentioned, that the expressions for both blended and alternative inheritance are obtained from the same series, which represent the gametic composition, suggests that we may possibly obtain cases of blending in character which normally follow the law of the alternative inheritance, and vice versa, and further we may even obtain both blended and alternative inheritance in the same offspring by subjecting the hybrid parents to different conditions, provided by such treatment we can modify the behaviors or functional activity of the de-

terminants, since as soon as the behavior is altered, we at once obtain from the series (2) another type of inheritance.

Although we have no clear direct evidence which demonstrates an occurrence of such extreme modification in the behavior of determinants, nevertheless the possibility of such an event is amply suggested by the recent experiments. For instance Tower ('10) has shown not only a reversal of dominance and apparent failure of segregation by merely modifying the environment of the beetles, but also a case in which the same parents produce offspring, some of which follow the law of Mendel while others show entirely different behavior with respect to dominance and segregation. Tennent ('10) was able to obtain from a cross of *Hipponoë esculenta* with *Taxopneustes variegatus*, reversal of dominance by decreasing the alkalinity of the sea water. Numerous samples of this sort can easily be found in the recent literature.

Whatever be the real condition or conditions which control the behavior of the determinants, one point is clear from the above, that the determinants are not immutable in their behavior, but subject to modification. This fact naturally leads us to think that we may obtain various forms of inheritance which are more or less different from the type form according to degree of functional modification. When a modification is maximum, we may even obtain a case of blended inheritance in a character which normally follows the law of alternative inheritance, or vice versa.

The facts mentioned above then indicate that our deduction from the properties of the formula is not at all improbable.

Again the properties of the formula suggests that we can theoretically connect cases of blended inheritance with those of alternative inheritance by the mere assumption that p or q fails to dominate either completely or incompletely. Since as we have shown by the degree

of dominance, the formula reduces to either equipotent or prepotent blending inheritance. From this standpoint we may consider that blending inheritance is a limiting case of alternative inheritance where either dominance is absent (equipotency) or is imperfect (heteropotency). If this hypothesis is accepted, then Mendel's law of alternative inheritance may be taken as the standard, and all cases referred to it or blending inheritance (though by this some more important features of inheritance are not suggested) may similarly be made the standard, the Mendelian ratios then becoming a special case.

In this connection Professor Davenport's ('07) view on the law of potency is of great interest. As his view of potency is so important, and especially as it clearly explains the relation between Mendelism and cases considered to be non-Mendelian, I shall quote his words at some length.

After quoting various cases of inheritance, Professor Davenport says:

Taking all cases into account, it is clear that Mendel's law does not cover all; and if not, it must be a special case of a more inclusive law. Can we find a more general expression for the inheritance of characteristics which will cover all these cases? I think we can and that it may be called the law of potency. At the one extreme of the series we have equipotent unit characters, so that when they are crossed, the offspring show a blend, or a mosaic between them. At the other extreme is allelopotency. One of the two characteristics is completely recessive to the other. Between the two extremes of equipotency and allelopotency lies the great mass of heritable characteristics which when opposed in heredity, exhibit varying degrees of potency. This sort of inheritance may be called heteropotency.

Thus Professor Davenport shows also that Mendelian dominance is a particular case of potency, allelopotency, though he did not state that blending inheritance is a limiting case of Mendelism.

Whether a new expression "the law of potency" should be introduced as Professor Davenport has suggested, or whether the various potencies may be consid-

ered as a limiting case of Mendel's law of alternative inheritance, thus saving the original name, is a matter for later decision, though the latter name seems to me more appropriate to retain owing to the fact that the phenomenon of segregation, most important of all, had been first stated by Mendel.

Let us now consider a limiting case of our formula (2) when the values of n (number of allelomorphic pairs of characters) increase. In the typical Mendelian ratio, the relative frequency of the various zygotes with respect to any given visible character is proportional to an expansion of $(1 + 3)^n$ which is the same as $(1/4 + 3/4)^n$ if we consider the relative values of the frequencies. Thus in all known cases of the inheritance, we have to deal with an expansion of $(r + s)^n$ where $r + s = 1$. A concise mathematical formula which represents a limiting case of the binomial series arising from an expansion of $(r + s)^n$ will be very useful, especially when we are dealing with a quantitative measurement such as weight, length, area, volume, etc., since in these cases the values of the variates will be graded. Further, the theoretical frequency corresponding to each variate when the value of n becomes very large, can best be determined from such a mathematical expression which represents a limiting case.

Without going into any detail of the mathematical treatment, it will be seen that we obtain two forms of expression according as $r = s$ or $r \neq s$. The former will be represented by the normal probability curve and the latter by a limiting case of a skew binomial curve. For representing a skew binomial curve we can best use DeForest's formula (Professor Pearson's curve of type 3). It may be useful to the reader to know that DeForest's formula degenerates into the normal probability curve as its simplest form, as will be seen below.

DeForest's formula (Hatai: '10) is usually written in the following form:

$$y = \frac{1}{k\sqrt{2\pi b}} \left(1 + \frac{x}{ab}\right)^{a^2b-1} e^{-ax},$$

where

$$k = 1 + \frac{1}{12a^2b} + \frac{1}{288(a^2b)^2} + \dots$$

a = quotient of twice the second moment divided by the third moment.

b = second moment.

Writing c for

$$\frac{1}{k\sqrt{2\pi b}}$$

we have

$$\begin{aligned} \log\left(\frac{y}{c}\right) &= (a^2b - 1) \log\left(1 + \frac{x}{ab}\right) - ax \\ &= (a^2b - 1) \left\{ \frac{x}{ab} - \frac{1}{2} \left(\frac{x}{ab}\right)^2 + \frac{1}{3} \left(\frac{x}{ab}\right)^3 - \frac{1}{4} \left(\frac{x}{ab}\right)^4 + \dots \right\} - ax \\ &= -\frac{x^2}{2b} + \left(\frac{x^2}{3b} - 1\right) \frac{x}{ab} - \left(\frac{x^2}{4b} - \frac{1}{2}\right) \left(\frac{x}{ab}\right)^2 \\ &\quad + \left(\frac{x^2}{5b} - \frac{1}{3}\right) \left(\frac{x}{ab}\right)^3 - \dots \end{aligned}$$

Since for a vanishingly small value of the third moment, ab will be a very large number, consequently x/ab will be infinitesimal. Thus neglecting all terms in which x/ab is factor, we have

$$y = ce^{-\frac{x^2}{2b}}.$$

Restoring the value of C and remembering that for large values of ab , k reduces to unity, we finally have

$$y = \frac{1}{\sqrt{2\pi b}} e^{-\frac{x^2}{2b}}$$

which is the familiar formula for the normal probability curve.

From the above it is clear that DeForest's formula and its limiting case represent the frequency distribution of the zygotes, whether we are dealing with alternative or

blended inheritance. One, however, must not be misled to conclude that continuous variation necessarily means failure of segregation, since on the contrary apparent continuity may be a resultant of combinations of various segregating characters. Whether or not given data indicate a segregation, may be variously tested by some other means according to the nature of the experiment.

From the above we draw the following conclusions:

1. The series obtained from the square of the binomial expresses the distribution of determinants for both alternative and blended inheritance.

2. Blended inheritance may be considered to be a limiting case of alternative inheritance where dominance is imperfect. Thus Mendel's law of alternative inheritance may be considered as the standard and all other cases referred to it.

3. DeForest's formula with its limiting case adequately represents frequencies of all known cases of inheritance when the number of allelomorphic pairs of characters is large, especially when quantitative measurements are considered.

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DATA ON THE RELATIVE CONSPICUOUSNESS OF BARRED AND SELF-COLORED FOWLS¹

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I. PHYSICAL DATA

THE purpose of this note is to put on record a rather striking physical fact, and to discuss briefly its biological significance. Some two years ago Davenport² published a short note regarding the relative number of self-colored and of "penciled or striped" chicks killed by crows one afternoon, at Cold Spring Harbor. The rather striking result was that out of 24 birds killed, only one was other than self-colored. The communication closes with the following words: "This fragment, then, so far as it goes, indicates that the self-colors of poultry, which have arisen under domestication, tend to be eliminated by the natural enemies of these birds, and the pencilled birds are relatively immune from attack because relatively inconspicuous."

Some photographs taken on the poultry range of the Maine Experiment Station this past summer illustrate this point made by Davenport as to the relative conspicuousness of self-colored birds in so striking and complete a manner as to warrant their publication and a critical discussion of their significance. These photographs were made without any thought whatever at the time that they were going to bring out the relative conspicuousness of different plumage patterns. Indeed, it was not realized that they did so until the finished prints were given to me by the station photographer, Mr. Roy-

¹ Papers from the Biological Laboratory of the Maine Experiment Station, No. 23.

² Davenport, C. B., "Elimination of Self-Coloured Birds," *Nature*, Vol. 78, p. 101, 1908.



FIG. 1. Photograph of a Golden Pencilled Hamburg ♂. Practically a solid colored bird (red on body, black tail). The few barred feathers which the ♂ of this variety has are covered by solid colored feathers. In this picture one barred feather shows in the region of the saddle. The wind had displaced this feather.

den Hammond, to whom I am indebted for developing and printing these pictures. As a matter of fact the four pictures which accompany this note were taken for the purpose of (a) testing a then new camera as to its usefulness in obtaining pictures to form part of a permanent record system in poultry-breeding experiments, and (b) to get photographic records of certain particular birds of interest from one standpoint or another. All the exposures were made by the same person (the writer) on the same afternoon and within an hour of each other. It was on a cloudless afternoon early in August, and the light conditions, shutter-opening, speed, and diaphragm opening were constant for all of the pictures. What differences appear in the pictures, then, are such as are referable to the different color patterns of the birds, when seen under the light conditions and against the kind of background which obtained in this case.



FIG. 2. A very dark, practically solid black F_2 ♂ from the cross Cornish Indian ♂ × Black F_1 ♀ from Cornish Indian ♂ × Barred Rock ♀.

From these photographs the following points are to be noted:

1. As compared with self-colored birds the barred individuals obviously are relatively much less conspicuous, when under the same light conditions, and when seen against the same kind of a background. The pictures of the barred birds (Figs. 3 and 4) are not, to be sure, like the "puzzle" pictures of supposedly protectively colored organisms, which one sometimes sees, where it is exceedingly difficult to distinguish the animal from the background at all. In both Figs. 3 and 4 it is easy enough to see the bird, but at the same time these birds are obviously much less conspicuous than those shown in Figs. 1 and 2.

2. This inconspicuousness is equally marked whether the barred bird is in the bright sunlight (Fig. 3) or in a relatively deep shadow (Fig. 4).

3. These pictures furnish objective and unbiased phys-



FIG. 3. An F_2 barred cross-bred chick. Sex ♀. Produced by mating F_1 barred cross-breds *inter se*.

ical evidence regarding the relative conspicuousness of two types of plumage pattern.

II. DATA ON THE BIOLOGICAL VALUE OF THE INCONSPICUOUSNESS OF THE BARRED PATTERN

The physical fact set forth above is obvious: barred chickens are clearly less conspicuous than self-colored when seen against the background of grass on the range where they live. Has this physical fact any biological significance? Are the barred birds, by virtue of the possession of this color pattern, at any advantage in the struggle for existence? Is their relative inconspicuousness any real protection against their natural enemies? It is the purpose of this section of the paper to present some numerical data regarding this matter.

The only evidence which exists in the literature on this problem, so far as poultry is concerned, consists in the admittedly fragmentary statistics presented by Davenport, which have been cited above. It should be pointed

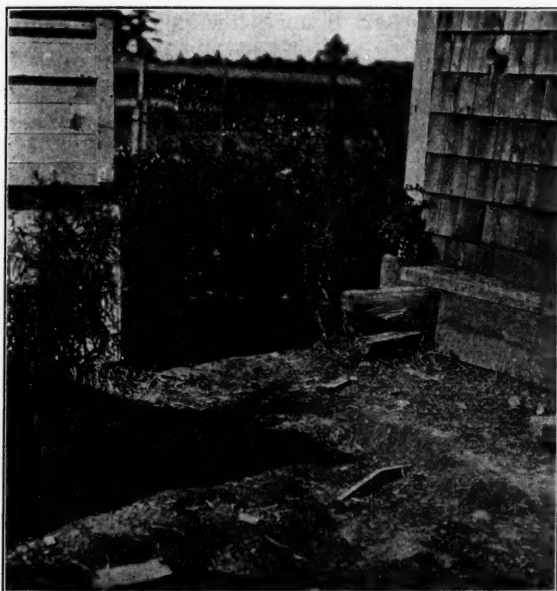


FIG. 4. A pure Barred Plymouth Rock ♀, with barring of fine quality from the fancier's standpoint. It is to be noted that the bird in this figure is in the shadow of a building in contrast to that shown in Fig. 3, which is standing in the bright sun.

out that Davenport's data are fragmentary not alone in respect to the small number of deaths (eliminations in the technical sense) involved, but also because these deaths were due to but a single one of the natural enemies of poultry, namely the crow. There are, of course, many others. Under the conditions prevailing on or about the poultry plant of which the writer has charge the following animals are regular or occasional destroyers of young chicks: Rats, skunks, foxes, crows, hawks, cats.³

In different seasons the relative importance of these different enemies varies. Thus in the breeding season of 1908 many birds were killed by foxes. In 1909, the year

³To this list one feels tempted to add that species of vermin which is in some respects the worst which attacks a poultry plant, namely the thief, but fortunately the *range* was free from his depredations in 1909.

for which statistics are given below, not a single bird was killed by a fox so far as is known. Similarly in 1909 no birds were killed by skunks. In 1910 a skunk succeeded in getting into a house one night and killed a number of birds. On the Maine Station plant normally predaceous birds undoubtedly rank first in destructiveness. This is probably quite generally true of poultry plants, though because of the fact that the loss is distributed so evenly over the whole season the importance of this class of enemies is apt to be underrated. Next to predaceous birds stand rats, under our conditions. An important point to be noted is that on the plant under discussion here all killing of chickens by rats is done in the daytime. Rats burrow in the ground under the houses, and then when the chicks are playing about a rat will dash out, seize a chick and carry it back to the burrow. It is not an uncommon occurrence for a rat thus to kill as many as 12 chickens within the space of an hour. With rare exceptions we never lose any chickens at night except those taken by thieves. The chicks are shut and locked in rat and (usually) vermin proof houses at night. Occasionally, as noted above, a skunk is able to effect entrance into a house. This, however, did not happen in 1909, the year which furnished the statistics given below. It should be clearly understood that in the statistics which follow all "eliminations" occurred in the daytime, when color and pattern might presumably be of some significance.

It is my purpose to present some statistics, involving a relatively large number of individuals, regarding the relation of color pattern to the elimination of chickens by all of these natural enemies taken together. These statistics cover the hatching season of 1909 in which chickens were on the range, and subject to the attacks of enemies, from about April 1 to October 1. Birds of all colors and patterns ran together on the same open, turf-covered range, and, without regard to color or pattern, all were equally exposed to attack by all sorts of

natural enemies. The total number of chickens involved was 3,343. An account of the way in which the statistics were obtained is necessary. All of these 3,343 chicks were of known pedigree, and a numbered aluminum leg band was attached to each one when it was removed from the incubator in which it was hatched. A record was made of each chick's number. This numbered leg band was worn by the chick throughout its life. Whenever a chick died a record of this fact was made opposite its entry in the pedigree book. During the season every living chick on the range was handled over twice and its leg band number checked back with the original entry, and at the end of the season all chicks remaining on the range were checked up.

Now it is clear that dead chicks which come to autopsy will fall into two general classes: on the one hand, those that died from one or another of the many *diseases* which make the poultry raiser's life a burden in the springtime, and on the other hand, those *killed by some enemy but not carried away*. In the latter class will fall the great majority killed by rats, some killed by skunks, and a fair proportion of those killed by foxes. Usually a direct record can be obtained for practically none of the chicks killed by predaceous birds and cats. In 1909 we have reason to believe that substantially all unrecorded deaths were caused by predaceous birds.

At the end of the season when the birds are checked up all will be accounted for as either (a) living, (b) dead from some disease, (c) killed by recorded enemies, or finally (d) missing. Of the missing birds there are two classes again. On the one hand are those killed by enemies which carried the carcasses away, and on the other hand, are those that through accident lost their leg bands, and hence, while present in the flock, can not be entered upon the records. With the methods of work in use here the number of the latter class has always been small. Unfortunately I am not able to give exact figures for such birds for the season of 1909. It can be stated with cer-

tainty, however, that they did not exceed 25. Of this number that lost their leg bands 8 were known to be self-colored birds.

There were on the range in 1909 three classes of birds, in respect to color pattern. These were (a) barred birds, bearing either the pattern of the pure Barred Plymouth Rock, or a modification of it;⁴ (b) solid (self-colored) black birds, resulting from the cross Cornish Indian Game ♂ × Barred Rock ♀; and (c) pure Cornish Indian Games of the dark variety which may for present purposes be classed as self-colored birds.

With this somewhat lengthy explanation of the composition of the flock and method of keeping records in hand we may proceed to examine the statistics of elimination. In compiling these statistics the blank birds which lost their bands (ca. 25) have been included with the eliminated. This does not affect the conclusions in any way because of the facts that (1) the number of such birds is so small relatively, and (2) the proportion of self-colored to barred birds among those which lost their bands is relatively higher than in the general population from which they came. The significance of this point will be apparent as we proceed.

We have the following figures, it being understood that "eliminated" means "killed by natural enemies" with the inclusion of the small number of birds which lost their bands as noted above.

Total number of birds = 3,343.

Number of *barred* birds = 3,007.

Number of *self-colored* birds = 336.

Total number of eliminated birds = 325.

Number of *barred* birds eliminated = 290.

Number of *self-colored* birds eliminated = 35.

The above figures include *all* eliminated birds, those killed by recorded and unrecorded enemies together. If we take only those killed by recorded enemies, which

⁴ See Pearl, R., and Surface, F. M., "On the Inheritance of the Barred Color Pattern in Poultry," *Arch. f. Entwicklungsmech.*, Bd. XXX, Fest-Band für Roux), pp. 45-61, 1910.

under the conditions prevailing on the plant in 1909 means practically those killed by rats, we have:

Number of *barred* birds eliminated by recorded enemies = 68.

Number of *self-colored* birds eliminated by recorded enemies = 6.

From these figures the following proportions are derived: Of the *total number* of birds 10.05 per cent. were *self-colored*.

Of all the *eliminated* birds 10.77 per cent. were *self-colored*.

If we consider by themselves the birds eliminated by recorded enemies, we have:

Of the birds *eliminated by recorded enemies* 8.11 per cent. were *self-colored*.

Putting the figures in another way we have:

Of the *self-colored* birds 10.42 per cent. were eliminated by *all* enemies.

Of the *barred* birds 9.64 per cent. were eliminated by *all* enemies.

Of the *self-colored* birds 1.79 per cent. were eliminated by *recorded* enemies (chiefly rats).

Of the *barred* birds 2.26 per cent. were eliminated by *recorded* enemies.

Of the *self-colored* birds 8.63 per cent. were eliminated by *unrecorded* enemies (chiefly predaceous birds).

Of the *barred* birds 7.38 per cent. were eliminated by *unrecorded* enemies (chiefly predaceous birds).

The conclusion to be drawn from these figures, which involve a large number of individuals, is obvious. It is that *the relative inconspicuousness of the barred color pattern afforded its possessors no great or striking protection against elimination by natural enemies, during the season (April 1 to October 1) of 1909 on the poultry range of the Maine Experimental Station*. It might be objected that if the eliminations by predaceous birds alone could be separately recorded it would then be found that against this class of enemies the barred pattern had

great protective value, as suggested by Davenport's figures. This, however, can hardly be the case in the present statistics since if it be assumed that predaceous birds killed relatively few barred chicks and relatively many self-colored, then it must also be assumed that the other unrecorded enemies showed a *preference* for barred birds, since with all enemies taken together substantially equal proportions of both kinds of birds were eliminated. In other words, if we assume a selective elimination in the case of predaceous birds, we are obliged to assume an *equal* and *opposite* selective elimination on the part of other unrecorded enemies. There is no evidence on which such an assumption could be based.

These figures, of course, cover only one year's experience, and are in no wise conclusive, but general observation indicates strongly that essentially the same result would be shown in other years if it were possible to tabulate the figures. Unfortunately neither the records of 1908 nor 1910 can be used for this purpose. In 1908 there were almost no self-colored birds on the range. In 1910, owing to the location of the houses on the range and other circumstances which can not be gone into in detail, thieves were active on the plant and the birds taken were not a random sample of the flock in respect to color. 1909 was a fortunate year for such a study as the present one. The thieves confined their attention to adult stock on a part of the plant away from the chicks, and left the latter strictly alone.

Definitely controlled observations regarding the elimination of animals by natural enemies, covering a considerable number of individuals and anything like a complete range of enemies, are exceedingly scarce. The whole question of the interplay of factors in the "struggle for existence" constantly going on in the organic world has been discussed very largely from the *a priori* standpoint, throughout the whole period since the appearance of the "Origin of Species." The "rabbit with his legs a little longer," the "fox with the little keener

sense of smell," the "bird of dull colors which harmonized with the background," *et id genus omne*, have been made to do valiant service.

Ever since the first description, made by the Nuremberg miniature painter Röseler in 1746,⁵ of a case of presumably protective coloration, we have been prone to argue that because an organism was colored or formed in such a way as to be inconspicuous it was, therefore, necessarily *protected* from attack by its enemies to a greater or less degree. The logic of such reasoning is flawless. It *ought* to be protected. But a conclusion may be perfectly logical and still not true. In the study of protective coloration, including mimicry, it is essential that a discovery that an organism is to human eyes inconspicuous or not readily distinguishable from some other organism shall not be considered the final goal. Rather let such a discovery always be supplemented by an experimental or observational determination of whether this inconspicuousness really helps the organism, in actual practise, in avoiding elimination by natural enemies. It is worth noting that more than one recent critical student of these problems who has applied this method has brought to light results essentially similar in their general import to those set forth here.⁶

⁵ Cf. Müller, H., "Schützende Aehnlichkeit einheimischer Insekten," *Kosmos*, Jahrg. III, Heft 8, p. 114, 1879.

⁶ Cf. for example the chapter on "Colouration of Organisms" in Dewar and Finn's "The Making of Species" (New York, 1909), and still more recently the thorough critical study by Punnett on "Mimicry in Ceylon Butterflies, with a Suggestion as to the Nature of Polymorphism" (*Spolia Zeylonica*, Vol. VII, Part XXV, September, 1910, pp. 1-24, 2 plates).

SOME CONSIDERATIONS CONCERNING THE PHOTOGENIC FUNCTION IN MARINE ORGANISMS

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IN two very interesting papers, Professor C. C. Nutting¹ has brought forth evidence tending to show that in oceanic depths below the range of penetration of the sun's rays, there exists a dim, phosphorescent light, quite general in its distribution, radiated from various photogenic organisms of the abyssal regions, and having a definite and valuable significance for the life of animal forms at these depths.

That such a light actually exists is scarcely to be sanely doubted, in view of the evidence of the deep-sea explorations which have added so much to the knowledge of oceanic conditions. And that it has a purpose in the life of the forms inhabiting those portions of the ocean beds where it exists, seems to the writer equally undeniable, unless we accept Emerson's poetic reasoning that

"Beauty is its own excuse for being."

Just what its purpose may be in hermaphroditic, simple forms not provided with definite organs of sight, and indeed also in many higher forms, may, of course, still be a legitimate subject for investigation and consideration.

Professor Nutting's remarks have been of special interest to the writer in connection with some recent studies made by the latter on the general subject of biophotogenesis, with special reference to the Lampyridæ.²

¹ (a) "The Utility of Phosphorescence in Deep-sea Animals," *AMER. NAT.*, Vol. 3, 1899, pp. 792-799; (b) "The Theory of Abyssal Light," *Proc. VII Cong. Zool.*, advance reprint, 1910.

² *Amer. Journ. Physiol.*, 1910 Vol. 27, pp. 122-151; *Canad. Entomol.*, 1910, Vol. 42, pp. 357-363; *Popular Sci. Monthly*, 1910, Vol. 77, pp. 114-121.

The coloring and photogenicity of the organisms found in the depths of the sea show some similarities to the corresponding features of life on land.

Take the family Buprestidæ, of the genus Coleoptera, of the order of insects. The insects of this family are probably the most brilliantly colored of any of the beetles, and are colored quite as brilliantly as the insects of any other genus. The colors cover a quite wide range of metallic, polished, glistening greens, blues, reds, coppery and golden; many of the smaller species wear more somber dark blues, browns and blacks, but as a class they are brilliant and showy. Obviously, these colors would be invisible in the absence of light, and need a light of considerable intensity to bring out their full value. Now we find that almost without exception these Coleoptera are diurnal; they attain their maximum activity during the brightest daylight, and fly but little at night. But one species has been reported to be luminous, and unless this report is pretty definitely confirmed there is grave reason to doubt its authenticity.

Now let us consider the Lampyridæ: The beetles of this family of almost eleven hundred species are in the great majority of instances, luminous; the non-luminous species form a decided minority of the true Lampyridæ. They are also, in the great majority of cases, mainly nocturnal in habit, hiding out of the sunlight during the day; those species which are markedly diurnal in habit are also those which are non-luminous, or in which the luminosity is relatively slight. In coloration, they show none of the bright metallic, showy colors of the Buprestidæ; black, gray, brown and yellow-brown predominate, with occasional red markings, yellow stripes and indistinct lines and spots. In them, the photogenic function possesses at least two definite significances: (1) it is an adjunct of the sexual organism of the insect, rendered of value to them by reason of their nocturnal habits, and (2) it has a protective value. In the larvæ it might also be considered to have an aggressive value, in attracting the snails, etc.,

on which they feed, but this argument would not hold for the imagos, which are much more active.

Most of the above statements apply with equal force to the Pyrophorini, the luminous Elateridæ of the tropics; these insects are herbivorous, however, and the aggressive significance does not hold for them.

It would seem, then, very probable that similar conditions obtain in the abyssal region, with its dim weird, phosphorescent light. The light produced by the Lam-pyridæ has recently been shown by Ives and Coblenz³ to have the extremely high radiant efficiency of 96.5 per cent., against 4 per cent. for the best artificial illuminant. The spectrum of this light is a continuous band extending from the upper red to the lower blue with a maximum intensity in the yellow-green. This spectrum is of wider range than that of the sea-forms cited by Nutting,⁴ but can hardly be of less efficiency. The light of the Lam-pyridæ is generally stated to be yellow, or greenish; there are some slight variations among different species, but in the main the lights are similar; it seems that a great many of the marine organisms also give a light of similar tone. Therefore colors whose wave-lengths are within the limits of those of the emitted lights of these forms, would be distinguishable in such a biophotogenic light. Although we do not yet know the full details of the process of the production of light by living forms, it is not too much to assume that Nature has developed it to a point very near to the maximum possible efficiency, and if such is the case, the luminous oceanic forms could emit a very penetrating illuminating radiation with very little expenditure of energy, and though this light might not be of any considerable intensity, as judged by our eyes, it could undoubtedly serve as quite a useful light to the large-eyed denizens of the deep.

The photogenicity of *Salpa*, *Noctiluca* and other such simple forms, which are without definite organs of sight,

³ Bulletin of the U. S. Bureau of Standards, 1910, Vol. 6, pp. 321-336.

⁴ *Supra* b, page 10.

presents other difficulties. It is not, however, necessary to the faculty of perception of light that definite organs should exist. It is a quite well-known fact that certain worms, bacteria, and other low organisms are able to detect ultra-violet rays to which the human organism is wholly without sensible response, and yet these actinotropic (if a coined word may be pardoned) forms show no definite organs such as might be adapted to the receiving and recording of the very short wave-lengths of ultra-violet light. If, then, existing organisms are known to be affected by ultra-violet rays for which they have no special sense-organs, it is certainly logical to assume that they and other forms may also be susceptible to the longer and more easily discerned wave-lengths of visible light—especially when those wave-lengths comprise mainly the rays possessing the highest illuminating effect—and without the necessity for the existence of “eyes” or other definite light-receiving organs. As a matter of fact *Noctiluca*, and numerous other marine organisms have been shown to be susceptible to light, although they possess no specific organs for this function so far as we have been able to make out.

Another consideration as to the purpose of the light presents itself here. We must consider the nature of the medium in which these creatures live. Water does not lend itself as readily as does air to the diffusion of the particles which produce the sensation of smell; and hence while odors, or speaking more properly, from the standpoint of marine organisms, flavors or tastes undoubtedly exist in the ocean water, they could not, on account of the water currents, lack of diffusion, etc., serve the purpose which the odors of land animals serve of giving indication of the presence and location of the creatures. It therefore would not be unreasonable to assume that in the gregarious simple luminous marine forms, the photogenic function takes the place to some extent of the animal odors of land forms.

To sum up, then:

From analogy to terrestrial forms, the photogenicity and coloration of marine organisms must play some essential part in their life histories;

The absence of definite organs for the reception of the radiations of light may not necessarily indicate that the forms from which they are absent are insensible to these radiations;

The photogenic function in certain simple marine forms may replace the olfactory function of terrestrial forms, to some extent.

SHORTER ARTICLES AND DISCUSSION

COMPUTING CORRELATION IN CASES WHERE SYMMETRICAL TABLES ARE COMMONLY USED

IN studying the assortative mating of *Paramecium* I have found occasion to compute the correlation in many cases for which double or symmetrical tables are commonly employed. I have found that in such cases the use of symmetrical tables is quite unnecessary and the computations can be performed with much less labor without them. It will, therefore, be worth while to show how the use of symmetrical tables can be avoided.

When the two objects to be compared are alike, as when the two members, *A* and *B*, of conjugating pairs are examined, evidently either *A* or *B* might be entered in either the horizontal rows or the vertical columns of the correlation table. In such cases, the mean computed from the rows, and that computed from the columns are likely to differ, depending on which individuals were entered in the rows, which in the columns. If, for example, the larger individual is always entered in the vertical columns, the smaller in the horizontal rows, as in Table II, then the means and standard deviations of the two sets will differ much. As a result the coefficient of correlation computed in the usual way will show varying values, depending on how the pairs are entered in the table. From the collection shown in Table II we can by varying the method of entering the pairs get coefficients of correlation varying from 0.132 to 0.523.

Under such conditions Pearson (1901), Pearl (1907) and others enter each pair twice, once in the rows, once in the columns. This gives a "symmetrical" table, in which the sums of either the rows or the columns include all the individuals. This method is theoretically correct, since each individual functions both as "principal" and as "mate"; the coefficient of correlation computed from such symmetrical tables is the correct one. But such symmetrical tables are cumbersome and involve much labor. Pearl (1907) gives a formula by which the same coefficient can be obtained without making symmetrical tables, by computations involving the two means and standard

deviations and the coefficient of correlation found in the usual way.

But it is possible to find the correct coefficient of correlation from ordinary tables, and with much less labor than by either the use of symmetrical tables or by the method given by Pearl. To see how this can be done, it is well to examine a symmetrical table prepared for computation of the coefficient of correlation, such as is given in Table I. Here the large figures give the frequencies, while the subscripts in smaller type give the products of the deviations from the approximate mean (37). There are two main points to be considered: (1) How the quantity

	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	
30								1					1 ₃				2
31						1 ₂ 1 ₆							2 ₂				4
32													1 ₂				1
33					1 ₅ 2 ₂ 1 ₅		2				3 ₂						12
34				2 ₂ 2 ₂ 2 ₂ 1 ₃		1 ₂						2 ₂	1 ₂				12
35		1 ₂		1 ₅ 2 ₂ 2 ₂ 3 ₂		5 ₂		3 ₆									23
36		1 ₆		1 ₃ 3 ₂ 4 ₂		7	3 ₁	5 ₂ 6 ₂									30
37	1		2	1	4	7	8	7	4	3		3					28
38				1 ₃ 5 ₂ 3 ₁	7	4	2 ₂ 5 ₂ 5 ₂ 6 ₂ 1 ₆				1 ₆	40					19
39						5 ₂ 4	2 ₂ 2 ₂ 2 ₂ 2 ₂ 2 ₂										31
40				3 ₂	3 ₆ 6 ₂ 3		5 ₂ 2 ₂ 2 ₂ 2 ₂ 2 ₂ 1 ₅ 2 ₂										14
41		2 ₂ 1 ₂					5 ₂ 2 ₂ 2 ₂ 2 ₂										17
42		1 ₃			2 ₂		3	6 ₂ 2 ₂ 2 ₂					1 ₃				3
43								1 ₆	1 ₂			1 ₃					3
44					1 ₂					2 ₂							1
45								1 ₆									250
	2	4	1	12	12	23	30	38	40	19	31	14	17	3	3	1	250

TABLE I. SYMMETRICAL CORRELATION TABLE FOR THE LENGTHS OF 125 PAIRS OF *Paramecium aurelia*; each individual entered twice, once in the vertical columns, once in the horizontal rows. (Unit of measurement, 4 microns)

$S(xy)$ is to be correctly obtained; (2) how the mean and standard deviation are to be correctly obtained.

1. With regard to the first point, it will be observed that such a table is divisible by a diagonal passing from the upper left-hand corner to the lower right-hand corner into two halves which are in all respects duplicates as regards both frequencies and deviation products. (The frequencies through which the diagonal line passes are to be divided evenly between the two halves.) It is evident, therefore, that if we use only one of these halves

of the table in getting the sum $S(xy)$ we shall get just one half the sum we should get by using the whole table; the sum for the whole table would therefore be obtained simply by doubling this half-sum. Now, if in place of making a symmetrical table we enter always the larger member of each pair in the vertical column, the smaller in the horizontal rows, we shall get a table that is precisely one of these duplicate halves of the symmetrical table; this will be seen by comparing Tables I and II. The quantity $S(xy)$ from such a table will then be just half that from the symmetrical table; it may then be doubled, and the further computation will be identical with that for the symmet-

	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	A	B'	C						
30								1						1 ₁₂			2		2						
31					1 ₁₂	1 ₈							2 ₂₄				4		4						
32													1 ₁₀				1		1						
33				2 ₆	2 ₁₂	1 ₈	2				3 ₁₂						10	2	12						
34					1 ₉	2 ₉	1 ₉	1	1 ₉				2 ₁₃		1 ₁₂		9	3	12						
35						2	3	4	5		3 ₆						17	6	23						
36		Y					2 ₁	7	3 ₁	5 ₁	6 ₁						23	7	30						
37								2	7	4	9		9				20	18	38						
38									2 ₁	2 ₂	5 ₁	5 ₄	6 ₁		1 ₈		22	18	40						
39										1 ₄	2 ₉	2 ₉	2 ₁₀				7	12	19						
40											1 ₉	2 ₁₂	2 ₁₂	1 ₁₀	2 ₁₁		8	23	31						
41												1 ₁₆					1	13	14						
42														1 ₁₀			1	16	17						
43																		3	3						
44						X												3	3						
45																		1	1						
B									2	3	6	7	18	18	12	23	13	16	3	3	1	23	12	25	50

TABLE II. THE SAME TABLE SHOWN IN TABLE I, SAVE THAT EACH INDIVIDUAL IS ENTERED BUT ONCE—the larger member of the pair in the vertical column, the smaller in the horizontal row.

rical tables. Or (as we shall see) this half sum, which forms the dividend in obtaining the coefficient of correlation, may be divided by a number half as great as in the symmetrical tables, giving the same result.

It will further be seen that if in place of entering all pairs in the same way—the larger members in the columns, the smaller in the rows—we enter some or all of them differently, this will make no difference in the result. If in Table II, for example, the pair showing measurements 44 by 34 were entered in the reverse way, it would fall, no longer in the right upper quad-

rant, but in the left lower quadrant, at the point marked X. Here, as examination will show, it would receive the same subscript that it has now, and would count as negative, exactly as it now does. Again, suppose the pair 36 by 31 were similarly transposed; it would still fall in the left upper quadrant, at the point marked Y, where it would receive the same subscript as at present and count as positive, just as at present. And so of all other cases; the value of a pair is not altered in any way by changes in the way it is entered in the table. In making the table, therefore, the pairs may be entered only once and quite at random, or in any way that is convenient.

2. With regard to the mean and standard deviation, the apparent advantage of symmetrical tables is that they give us the actual mean of all the individuals; it is to this mean that our correlation must refer. But this actual mean can readily be obtained from the tables in which each pair is entered but once, in any way that happens to be convenient. It is merely necessary to add together the sums of the rows and of the columns of the table. Thus in Table II the number of individuals having the length 35 is not 17 (sum from the row beginning with 35), nor 6 (sum from the column headed 35), but 23 (sum from both the row and the column) and so for all other classes. It will be well to illustrate by an example certain of the steps in the computation. Table II shows a correlation table of single entry, as prepared for computation of the coefficients of correlation and other constants.

After finding the sums of the rows (given in column A at the right) and of the columns (given in B, underneath), we place the latter sums (B) by the side of A, in the proper places (as at B'), then add the two sets, giving the sums shown in the column C at the right. These are the same sums that we should get from a symmetrical table; adding these we get the total number of individuals (250 in Table II). Now from this column C we find the approximate mean in the usual way; it lies in this case at the length 37 (with 38 individuals). Through the column and the row headed 37 we therefore draw the lines serving as axes of reference in finding the correlation. We now find the correlation in the usual way. In so doing (1) we make use always of the sums in the column C in finding mean, standard deviation, etc. (2) We use for both horizontal and vertical axes of reference in computing the correlation in all cases

a row and column with the same heading (37 in this case).

(3) We employ the ordinary frequencies in the body of the table in getting the sum of the deviations of (xy) for use in the formula for the coefficient of correlation, just as in ordinary correlation tables. The computation of the coefficient is of course (as in the case of symmetrical tables) considerably simpler than in the usual case, since we have but one standard deviation and one quantity d to deal with.

Only one other point in the computation is peculiar, requiring careful observance. If we let n signify the number of pairs and N the number of individuals (so that $N = 2n$), then in finding the mean, standard deviation, and coefficient of variation, we use N (just as in symmetrical tables), so that the formula for the standard deviation is

$$\sigma = \sqrt{\frac{S(x^2)}{N} - d^2} = .083.$$

But in getting the coefficient of correlation, the sum $S(xy)$ which we get from our unsymmetrical table is just half what we should get from a symmetrical table (as we have already seen). Therefore, to make the computations identical with those for symmetrical tables, we must either double this sum in the formula for the coefficient of correlation, or what is simpler, in place of doubling this sum we may halve the number by which we divide this sum, that is, we may use n in place of N . Thus the formula for the coefficient of correlation becomes by this method

$$r = \left(\frac{S(xy)}{n} - d^2 \right) \times \frac{1}{\sigma^2}.$$

This method lends itself readily to the valuable procedure recently described by Harris (1910) for finding the coefficient of correlation, the only point requiring careful attention being the fact that in finding the standard deviation we must use N (number of individuals), while in the formula for the coefficient of correlation we must use n (number of pairs). The present plan is likewise well adapted for finding the coefficient of correlation by the "difference method" (see Harris, 1909).

If the method we have described is used, the pairs are entered in the table but once, in any way that is convenient; the correlation computed will always be the same, and identical with that from symmetrical tables. It avoids the cumbersome and labo-

rious symmetrical table; at the same time it involves much less labor than the method given by Pearl. When there are many tables to be computed, the amount of drudgery it saves is great.

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